Zitteliana	10	689–701	München, 1. Juli 1983	ISSN 0373 – 9627

Campanian and Maastrichtian Inoceramids: A review

By

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With 6 text figures

ABSTRACT

Late Cretaceous deposits of the Northern Hemisphere contain numerous Inoceramids. As "biostratigraphic tools" they are used with excellent results for strata of the Mid-Cretaceous and early Late Cretaceous. Inoceramids are just as frequent as in Mid-Cretaceous in strata of Late Cretaceous age (Campanian and Early Maastrichtian). Yet, on a wide geographic scale (Northern Hemisphere) they have not been used for precise dating. Data on inoceramid occurrence and distribution are available for many regions but in NW Germany and in most areas of the USSR, Campanian and Maastrichtian inoceramids have been studied much more thoroughly than in most other regions.

Biogeographically above the Lower Campanian, deposits of the Northern Hemisphere belong to two large entities: the North Pacific Province and the Euramerican Region (includes the European Palaeozoogeographic Province of NAIDIN and all North American deposits except those of the West Coast). In the North Pacific Province strata are subdivided biostratigraphically by inoceramids endemic to that region. In Maastrichtian deposits from temperate seas in the Northern Hemisphere, a subdivision can be made using the "aberrant" tegulated inoceramids: *Spyridoceramus tegulatus* occurs in Lower Maastrichtian strata, *Tenuipteria argentea* characterises Upper Maastrichtian strata. The Tethys fauna of Europe and Africa has many elements in common with the Euramerican region.

The extinction of the inoceramids has been a gradual process beginning in the Campanian; by Mid-Maastrichtian times only one genus survived which lived till the youngest Maastrichtian. The extinction in Early and Mid-Maastrichtian was not due to a sudden disappearance of favourable ecological conditions: "inoceramid-like" species are found after the disappearance of most inoceramid groups. In the Danian inoceramids and inoceramid-like species are unknown.

KURZFASSUNG

Die in den Oberkreide-Ablagerungen der Nord-Hemisphäre häufig auftretenden Inoceramen werden biostratigraphisch mit sehr guten Erfolg in Schichten älter als Santon eingesetzt. Obwohl Inoceramen auch in Schichten des Campan und Unter-Maastricht zahlreich vertreten sind, werden sie hier nicht zur Einstufung herangezogen. Aus vielen Gebieten liegen zwar Angaben über ihre Verbreitung vor, sie sind jedoch nicht immer überregional vergleichbar, da sie nur in NW-Deutschland und in der USSR gründlich untersucht sind. In der nordpacifischen Faunenprovinz wird das Campan mit endemischen Inoceramen unterteilt. Im Maastricht der gemäßigten Nordhemisphäre können die ,,aberranten" tegulaten Inoceramen zur Unterteilung eingesetzt werden: *Spyridoceramus tegulatus* für das Untermaastricht und *Tenuipteria argentea* für das Obermaastricht.

Biogeographisch gehören die Schichten jünger als Untercampan in der Nord-Hemisphäre zu zwei großen Einheiten: die ,,Nord-Pazifik"-Provinz und die ,,Euramerika"-Provinz (europäische paläozoographische Provinz von NAIDIN zusammen mit allen nordamerikanischen Vorkommen, außer der Westküste). Die Tethys-Faunen Europas und Afrikas haben viele gemeinsame Formen mit dieser Euramerika-Provinz.

Das Aussterben der Inoceramen vollzog sich schrittweise, beginnend im Campan. Im mittleren Maastricht überlebte nur noch eine Gattung, die bis zum Ende des Maastricht auftritt. Das Aussterben im Untermaastricht kann nicht auf das plötzliche Aussetzen von günstigen ökologischen Bedingungen zurückgeführt werden; ,,Inoceramen-ähnliche" Formen finden sich auch noch nach dem Aussterben der meisten Inoceramen-Gruppen. Aus dem Dan und höher sind Inoceramen und ,,Inoceramen-ähnliche" Arten unbekannt.

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RÉSUMÉ

Dans l'Hémisphère nord les dépôts néocrétaciques contiennent de nombreux inocérames. En biostratigraphie ils rendent de bons services jusqu'à la fin du Santonien. Dans les dépôts du Campanien et du Maastrichtien inférieur les inocérames restent tout aussi fréquents. Cependant à large échelle géographique (l'Hémisphère nord) ils sont inutilisables pour la datation précise. Dans des travaux régionaux nous trouvons de nombreuses données sur la présence et la distribution des inocérames; elles ne sont pas toujours comparables, parce que dans le Nord-Ouest de l'Allemagne et en URSS, les inocérames du Campanien et du Maastrichtien inférieur ont été étudié plus en détail que dans d'autres régions.

Après le Campanien inférieur les dépôts de l'Hémisphère nord forment deux grandes entités biogéographiques: la Province du Pacifique Nord d'une part et la Région Euraméricaine d'autre part (la Province Paléozoogéographique Européenne de Naidin, et les dépôts d'Amérique du Nord à l'exclusion de ceux de la côte ouest).

Dans la Province du Pacifique Nord la biozonation du Campanien se fait à l'aide d'inocérames endémiques à cette province. Dans les dépôts maastrichtiens de mers tempérées de l'Hémisphère nord la subdivision de cet étage peut se faire à l'aide d'inocéramidés «tégulés»: *Spyridoceramus tegulatus* caractérise le Maastrichtien inférieur, *Tenuipteria argentea* le Maastrichtien supérieur.

La faune téthysienne d'Afrique et d'Europe est très proche de celle de la Région Euraméricaine.

L'extinction des inocéramidés a été un processus graduel, qui a commencé au début du Campanien. Au Maastrichtien moyen un seul genre survit qui disparait à la fin du Maastrichtien. La disparition des inocéramidés au début du Maastrichtien n'est pas expliquable par une soudaine absence de conditions écologiques propices au groupe: des homéomorphes d'inocérames se trouvent, après la disparition des inocéramidés, dans le Maastrichtien moyen et supérieur. Au Danien on ne retrouve ni inocérames ni homéomorphes d'inocéramidés.

CONTENTS

INTRODUCTION

Among the macrofossils used for Cretaceous biostratigraphy, inoceramids have traditionally been important for the Mid-Cretaceous and early Late Cretaceous. In areas where ammonites are relatively rarely found, they are an excellent biostratigraphic tool, especially from the Turonian to Santonian. In the latest Cretaceous, Campanian and Maastrichtian, their biostratigraphic usefulness has generally been disclaimed. Yet, especially in the Campanian, inoceramids were still quite common.

It seemed interesting to check what happened on a wide geographical scale (Northern Hemisphere and Tethys) in the terminal Cretaceous, within the inoceramids: how their biogeographical distribution evolved, how their stratigraphical distribution changed, how their "extinction" took place.

I. GENERAL REMARKS ON INOCERAMIDS

Inoceramidae are recorded from the Early Permian to the latest Cretaceous. The biostratigraphic importance of this family of pteriacean bivalves is due to the genus *Inoceramus* J. Sowerby, 1814, which is known to have occurred from the Early Jurassic to the Late Maastrichtian. The number of species which have been assigned to the genus is huge: Pergament (1981) lists, on a worldwide basis 94 species (in a work on the Cretaceous-Tertiary boundary); 94 species for the Campanian and Maastrichtian stages alone – and in the Maastrichtian inoceramids are relatively rare! For an area limited to the Western Interior of North America, Kauffman (1975) lists 89 subspecies and species of inoceramids for the Campanian and Early Maastrichtian. According to the standards used by most mollusc workers, an average of 50 species in one genus per stage is exceptional, even in a genus in which species have short ranges (this indeed might mean close to 1000 species in the genus *Inoceramus* in its total range).

This is not a new problem: in the last 150 years authors have repeatedly attempted to subdivide the vast series of known *Inoceramus* species on morphologic, phylogenetic or other criteria. Thus *Mytiloides* as a genus/subgenus dates back to Brongniart, 1822, *Endocostea* to Whitfield, 1880. The first thorough attempt at subdividing and classifying all „*Inoceramus*" was made by Heinz (1932 and others). The result was

rather confused and confusing: the main problem created was of nomenclative nature as HEINZ often did not follow ICZN rules. Most later systematic studies on inoceramids are based on the best aspects of HEINZ's work. In the Treatise of MOORE, COX (1969) tried to define (in accordance with the ICZN) some of HEINZ's invalid but useful names.

For Cretaceous Inoceramidae less ambitious and less extreme subdivisions have been used: – informal groups based on morphologic characteristics (DOBROV and PAVLOVA, 1959); – systematic groups at the subgeneric level, applying many elements of the system introduced by HEINZ, but having redefined them (SEITZ, 1961 b, 1965, 1967, 1970, and SORNAY, 1966, 1969, 1973 etc.). Other authors such as TSAGARELY (1942, 1949) and KAUFFMAN (1973, 1977 and others) use genera/subgenera from HEINZ and from earlier authors: in KAUFFMAN (1977) *Cladoceramus, Endocostea* and *Platyceramus* have subgeneric rank and *Mytiloides* is given generic rank. Modern Soviet authors, as a rule, follow a system modified after DOBROV and PAVLOVA. All species belong to *Inoceramus* but the species are placed in "species-groups". Only *Tenuipteria* is occasionally granted generic rank.

MITURA (1957) explained why the study of *Inoceramus* is so difficult. The problem lies partly in the homogeneity of the group (which makes it very difficult to quantify the differentiating characteristics) and also the preservation is generally poor (which results in the absence of information on the characteristics of the shell and means that species often are only known as internal moulds). Yet, despite those preservational limitations some inoceramids are important stratigraphic tools. As demonstrated by KAUFFMAN (1975) their long pelagic larval stage ensured a very wide distribution (some species groups might well have been pelagic all through their life: pseudoplanktonic or epiplanktonic).

II. REGIONAL REVIEW

The geographical area considered is very wide. Obviously I am not as familiar with faunas from the Pacific Province as with those from Western Europe. Hence, the data have been collected with the usual bias (conclusions are drawn for a very large area but the author considers as central the area in which he works, on personal rather than on scientific grounds). South America and the Southern Pacific area (Australian Province of KAUFFMAN, 1973) are omitted.

The data available to-day on inoceramids from the Campanian-Maastrichtian stratigraphic interval cannot always easily be compared. The Campanian-Maastrichtian boundary is not always put in the same place by all authors (below or above the *B. polyplocum* Zone) and in some areas (such as N. Germany and many regions in the USSR) the group has been studied in greater detail than in others (such as France or Spain or most areas of the USSR).

1. GERMANY AND NEIGHBOURING AREAS

The first basic stratigraphic work on Late Cretaceous Inoceramids was done in Germany a. o. by ANDERT (1911), J. BOEHM (1911, 1915), G. MUELLER (1900). Those early authors generally limited themselves to the Turonian-Coniacian (= Emscher) interval. Logically they worked on the strata in which the inoceramids are most numerous. Later authors HEINE (1929), HEINZ (1928, 1932), RIEDEL (1931) worked on stratigraphically younger levels and included the Santonian. At that time in much of Northern Europe the Campanian-Maastrichtian interval was divided in "Mammillaten"- and "Mucronatensenon" and no major boundaries in that interval were based on inoceramids. In the early 1950's under the influence of the Russian school (ARKHANGELSKY [1912], SCHATSKY, but mainly through JELETZKY [1951 and others]) the "Mucronatensenon" was biostratigraphically subdivided on the base of its belemnite content by SCHMID (1955a and b, 1956) and German uppermost Cretaceous strata were subdivided according to international usage. In connection herewith GIERS (1964) and SEITZ (1956, 1965, 1967, 1970) concentrated also on inoceramids of Campanian age. Only SEITZ made occasional references to inoceramids of Maastrichtian age. This neglect is understandable since Maastrichtian deposits are much rarer in Germany than those of Campanian age. Nevertheless, SEITZ made the only virtually complete study of inoceramids occurring in late Late Cretaceous age in Europe. His results apply widely in the European Palaeozoogeographic Province (or as it is generally known E.P.P. of NAIDIN [1959]) and probably also beyond that region.

It is especially interesting to connect the northern German data with those of Denmark and southern Sweden, using the data on Höllviken (BROTZEN, 1945, ØDUM, 1953) and the generally well studied Danish section (BIRKELUND, 1957, W. KEGEL CHRISTENSEN, 1975, 1976, RAVN, 1902, SURLYK, 1972, SURLYK and BIRKELUND, 1977, TROELSEN, 1937).

2. ENGLAND

In England, just about all Cretaceous bivalves were revised in WOODS' monumental monograph (1899–1913); due to insufficient stratigraphic resolution (typical of that period) the data given for inoceramids are no longer satisfying to-day (see also KAUFFMAN, 1976). Still, the fact remains that WOODS was the first worker on Cretaceous bivalves who gave good illustrations of real specimens (and not synthetic reconstructions as were made all too frequently in the monographs of GOLDFUSS or D'ORBIGNY).

It is unfortunate that till to-day no revision of English Cretaceous inoceramids has been published. WOODS' inoceramids have – because of the accurate illustrations – been reinterpreted by many inoceramid specialists and often by persons who had not seen the specimens. As a result different species concepts have been applied to the same name.

Most of the Campanian inoceramids from Late Campanian deposits described by WOODS seem to belong to the *Inocera-*

mus balticus s. l. species group which also occur in the underlying *quadratus* chalk. An exception is the species which WOODS described as *I. inconstans* var. *sarumensis* which was considered by HEINZ (1928) and later by TSAGARELY (1942) and by ATABEKIAN and BOBKOVA (1974) as a distinct species – *I. sarumensis*. The species which are limited to the *quadratus* Zone *I. cardissoides* GOLDFUSS, *I. lingua* GOLDFUSS, *I. lobatus* GOLDFUSS, *I. pinniformis* WILLETT, *I. tuberculatus* SCHROEDER, all can be considered as belonging to the subgenus *Sphenoceramus* as understood by SEITZ (1965).

Maastrichtian deposits on land in England are rare.

3. BELGIUM – THE NETHERLANDS

In the Belgian-Dutch Campanian the geographic situation is intermediate between Northern Germany, England and the Paris Basin. The first study ever published on the Campanian inoceramids was made recently by SORNAY (1982) on the specimens of the coll. of the I.R.Sc.N.B. It shows the following picture: for the topotypical "Smectite de Herve" (early Late Campanian) the most frequent species belong to the *I. balticus* group. In deposits probably of the same age in Limburg (coal mine shaft) many species belonging to *Platyceramus* have been found, along with the *I. balticus* group. In the uppermost Campanian-possibly Lower Maastrichtian strata of Hainaut, SORNAY also describes *I. pteroides pyrenaicus* SORNAY and *I. inordinatus* (HEINZ). Thus we are confronted with a fauna of mixed affinities – containing elements of the North German Campanian but at the same time species found in the Charente and Aquitaine. Most elements are within the *Endocostea* subgenus. For the stratotypical Maastrichtian *Tenuipteria argentea* (CONRAD) has been recorded (DHONDT, 1979, 1982 and 1983).

4. FRANCE

The most comprehensive monograph on Cretaceous bivalves is by D'ORBIGNY (1844–1847). After this basic work very little fundamental work on inoceramids was done in France until 1950 (SORNAY, 1959). Since then SORNAY published fairly extensively on inoceramids from French and African Upper Cretaceous deposits: on the Campanian-Maastrichtian interval in 1957, 1962, 1966, 1973, 1976, 1978. He used the descriptive system derived from HEINZ, also used by SEITZ. During the last thirty years SORNAY has not only published systematically but has also identified specimens for many authors publishing stratigraphic papers on deposits of Late Cretaceous age: hence a unity now exists in French inoceramid usage and nomenclature for strata of Middle and Late Cretaceous age. However, comparing the results of inoceramids from Campanian-Maastrichtian strata in France with similar inoceramids from the rest of Europe, is not always easy. In France the Maastrichtian stage is very often still understood as it was defined by HAUG (1911) whereby the first Maastrichtian zone is the *B. polyplocum* Zone. In the generally accepted international usage the *B. polyplocum* Zone is the last Campanian zone (ATABEKIAN, 1979). In the Charente, Aquitaine, the Pyrenees and S. E. France belemnites are absent, hence the correlation with N. and E. Europe is difficult. Most of the inoceramids described from those areas are of the *I. balticus* group s. l. and also of the *Platyceramus* group.

Only from the Cotentin undoubted Maastrichtian deposits with numerous bivalves are known in the "Craie à Baculites". BIGNOT and LARSONNEUR (1969) assigned by microfossil data a latest Campanian-Maastrichtian age to these deposits. SORNAY (1973) described a new *Trochoceramus* species from these strata: *Tr. morgani*. In the BM(NH), collection de Gerville, this *Trochoceramus* species and *Endocostea* specimens (group *balticus)* are present from the same strata in the Cotentin.

5. IBERIAN PENINSULA

Campanian-Maastrichtian inoceramid-bearing strata are not frequent in Spain and seem to be largely restricted to the Pyrenean region. SORNAY (1978) described a few species from there belonging to *Platyceramus* and *Endocostea* s. l.

6. USSR

In the vast territory of the USSR, marine deposits of Late Cretaceous age are widely distributed- indeed they are present from the most eastern to the most western part of the country. The stratigraphic subdivisions have been partly based on belemnites for a long time, and already ARKHANGELSKY (1912) used belemnites much as we do to-day.

At present, just about all Upper Cretaceous deposits of the USSR have been studied. For most regions inoceramids have been worked on both stratigraphically and systematically. A more or less uniform stratigraphic scheme is now in use (PERGAMENT, 1978). Examples of detailed regional studies of deposits and inoceramids of terminal Cretaceous age: Far East of the USSR: PERGAMENT (1974), ZONOVA (1970), Ukraine: KOCIUBYNSKII (1968, 1974), Crimea and Caucasus: DOBROV and PAVLOVA (1959), Georgia: TSAGARELY (1942, 1949), GAMBASHIDZE (1979), Armenia and Daghestan: EGOAN (1955), RENGARTEN (1965), ATABEKIAN and BOBKOVA (1974), Azerbaydzhan: ALIEV (1939 and others), Kopet Dagh: ATABEKIAN and LICHATSHEVA (1961).

In Campanian-Maastrichtian times, large areas of the western USSR are part of E. P. P. (NAIDIN, 1959 and this volume).

The Far Eastern USSR are part of the North Pacific Province; in the Campanian this area is characterised by an inoceramid fauna which is partly "endemic" and in the Upper Campanian the *I. schmidti* Zone is based on one of those Northern Pacific inoceramids.

7. BULGARIA

In Bulgaria, Campanian-Maastrichtian strata contain many inoceramids. Those are and have been studied by JOLKIČEV (1962 and others). They seem to have some relation with the faunas from the Charente.

8. AFRICA

The evolution of geology and palaeontology on the African continent has been connected with colonial enterprise. Two phases, which both resulted in important research for Cretaceous inoceramids, can be distinguished:

a. period of discovery expeditions (around 1800 to 1914): in pre-or early colonial times, many, sometimes surprisingly large, expeditions were organised: their aim was to collect general scientific information. During some of the earlier ventures two important Cretaceous oysters were discovered: *Exogyra africana* (LAMARCK, 1801) and *Exogyra overwegi* von BUCH, 1852. When the discovery expeditions became more frequent, geological (and palaeontological) studies were published on many regions. A few examples for the Cretaceous: on northwest Africa: BAYLE in FOURNEL (1849), COQUAND (1862), PÉRON (1890–1891), PERVINQUIÈRE (1912); on northeast Africa: the expedition of Rohlfs in the "Libysche Wüste" (Libyan Desert) (1873–1874) collected material of Mesozoic and Cainozoic age which was studied under the direction of ZITTEL (1883, 1893–1902); on Cameroon: von KOENEN (1897); on Gabon: KOSSMAT (1893); on Angola: CHOFFAT (1898); on Tanzania – the famous Tendaguru expedition (which collected the Brachiosaurus and transported it from the Tendaguru to near the coast of the Indian Ocean without the help of any kind of vehicle, 1914: publication of the results on invertebrate faunas).

b. 1914 until to-day: after the establishment of colonial rule many administrations started geological surveys. Systematic geological research and mapping was undertaken by these new surveys (in later days often in collaboration with oil-companies). To-day in the now independent countries the same kind of research is continued by the national geological surveys. Some examples of Cretaceous macrofossil research undertaken in such circumstances: Cameroon: RIEDEL (1932), Ghana: COX (1952), Nigeria: REYMENT (1955), West Coast of Africa: SORNAY in DARTEVELLE and FRENEIX (1957), Malagasy Republic (Madagascar): COLLIGNON (1951 and others), SORNAY (1968, 1969, 1973), Ethiopia and Somalia: TAVANI (1947–1948), Libya (Cirenaica and Tripolitania): PARONA (1923), NALDINI (1949), TROEGER and RÖHLICH (1980, 1981).

The african inoceramids known from the Campanian-Maastrichtian interval are for North and West Africa definitely close to those of the European Tethys. Those areas were connected through the sea between Algeria-Tunisia-Libya to the north and Nigeria to the south. This seaway continued as far as Angola along the West Coast of the continent. Also along the East Coast of Africa the connection with Tethys must have been fairly easy: some inoceramid species are in common between Madagascar and Libya (TROEGER and RÖHLICH, 1980).

It is difficult at this point to judge in how far inoceramids of Africa are different from those of European Tethys. HEINZ (1933) and SORNAY (1968 and 1973) express partly contradictory opinions. The results of TROEGER on Libyan material might give us the answer in the near future, in case more species are found which occur both in Madagascar and in Libya.

9. NORTH AMERICA

The Cretaceous deposits of the West Coast of North America (USA and Canada) belong to the North Pacific Province (see under that heading). The other Campanian-Maastrichtian deposits in North America are found on the Atlantic and Gulf Coastal Plains and in the Western Interior Seaway (as it was in the Cretaceous). Inoceramids are numerous in the Western Interior deposits (see GILL and COBBAN, 1966 for a detailed description of the Red Bird Section in Wyoming indicating the precise distribution and location of the inoceramids within the section; also KAUFFMAN, 1975). In the Atlantic and Gulf Coastal Plains these inoceramid-bearing deposits are less frequent. Except for the *Tenuipteria*-species revised by SPEDEN (1970), the work on Campanian-Maastrichtian inoceramids of the USA is not very advanced: W. A. COBBAN made the following statement (written communication of April 11, 1982): "Regarding the last of the inoceramids, nothing has been written about them except for the original descriptions of Meek and Hayden. I am referring to the group of *Inoceramus (Endocostea)* and not *Tenuipteria.*" For Canada, DOUGLAS (1942) described inoceramid species from the Bearpaw (Upper Campanian). In the Western Interior marine Upper Maastrichtian deposits are generally considered as missing. In the Gulf and Atlantic Coastal Plains Upper Maastrichtian deposits are present ("Prairie Bluff" and "Owl Creek"). The only inoceramid species from those strata seems to be *Tenuipteria argentea* (CONRAD) which tallies with Europe and Central Asia (DHONDT, 1982b).

10. NORTH PACIFIC PROVINCE

This biogeographic province was defined by JELETZKY (1965) and includes Japan and regions in the Far East of the USSR, Alaska, parts of British Columbia in Canada, and deposits on the West Coast of the USA. Campanian and Maastrichtian deposits occur on the Asian side of the province. Campanian is well documented in British Columbia (JELETZKY, 1971 and others), in Northern Alaska (JONES and GRYC, 1960). Deposits of Early Maastrichtian age are also found in California (MATSUMOTO, 1960) and probably in Southern Alaska (JONES, 1963).

Inoceramids endemic to this province are used for biostratigraphical purposes in the Campanian: *I. naumanni* Zone and *I. schmidti* Zone are two of the better known zones (JELETZKY, 1971 and PERGAMENT, 1978). For Maastrichtian biostratigraphy species such as *I. shikotanensis*, *I. kusiroensis* and *I. tegulatus* s. l. (PERGAMENT, 1974, 1978) are indicated. Their frequency seems to be low.

There seems to be no possible doubt that as suggested by JELETZKY (1971) this North Pacific Province was an entity separated at least partially from the Tethys and probably virtually not influenced by the temperate faunas of the Northern Hemisphere occurring from the Western Interior of North America over large parts of Northern Europe into Central Asia (see also textfigs. 2, 3, 4, 5, 6).

III. STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

Figure 1 indicates the stratigraphic extension of the systematic entities (genera, subgenera, or "species-groups") occurring in the Campanian-Maastrichtian of the Northern Hemisphere and Tethys. The systematic entities used do not have a completely formal delimitation and are largely taken out of SEITZ (1961 b, 1965, 1967, 1970). The data on which this distribution is based have been compiled partly after personal research and/or collecting but for the larger part they have been taken out of literature (see the articles mentioned in the regional reviews). The groups considered do not have the same extension in all regions. For figure 1 I have used the maximum extension. Three groups are common in the Campanian above the *pilula* Zone: *Cordiceramus*, *Platyceramus* and *Endocostea* s. l. All three are long-ranging (Santonian to Maastrichtian) and seem to cross the Campanian-Maastrichtian boundary without hesitation. However, in the Maastrichtian their distribution can be more restricted geographically and the number of species can be much more limited also. An example of such restriction in distribution is *Cordiceramus* (figure 2): in the Maastrichtian this subgenus is known from Nigeria *I. coxi* REYMENT, 1955) but as far as I have been able to ascertain not from anywhere else. *Platyceramus* (figure 3) is known from several Maastrichtian localities, but largely within the Tethys deposits – and often the correlation of those deposits with those of temperate seas still leaves something to be desired. *Endocostea* s. l. (figure 4) apparently undoubtedly occurs in the Lower Maastrichtian deposits both in North America and in Europe and Africa. The distribution during Maastrichtian times seems to have been less wide than during the Campanian but this might simply be due to the fact that there are fewer Maastrichtian than Campanian deposits known. *Trochoceramus* (figure 5) is a group which probably arose in Mid to Late Campanian times. Its distribution is interesting: it is quite common in the Tethys and the larger part of the occurrences in temperate seas are at the southern border of those seas (exception: Rügen). I have not found American species which could be placed in this group. The absence of *Trochoceramus* in North America could be the result of the widening of the Atlantic Ocean. However, this seems unlikely when the groups *Spyridoceramus* and *Tenuipteria* (figure 6) which originated later existed on both sides of the same Atlantic Ocean. These more widely distribu-

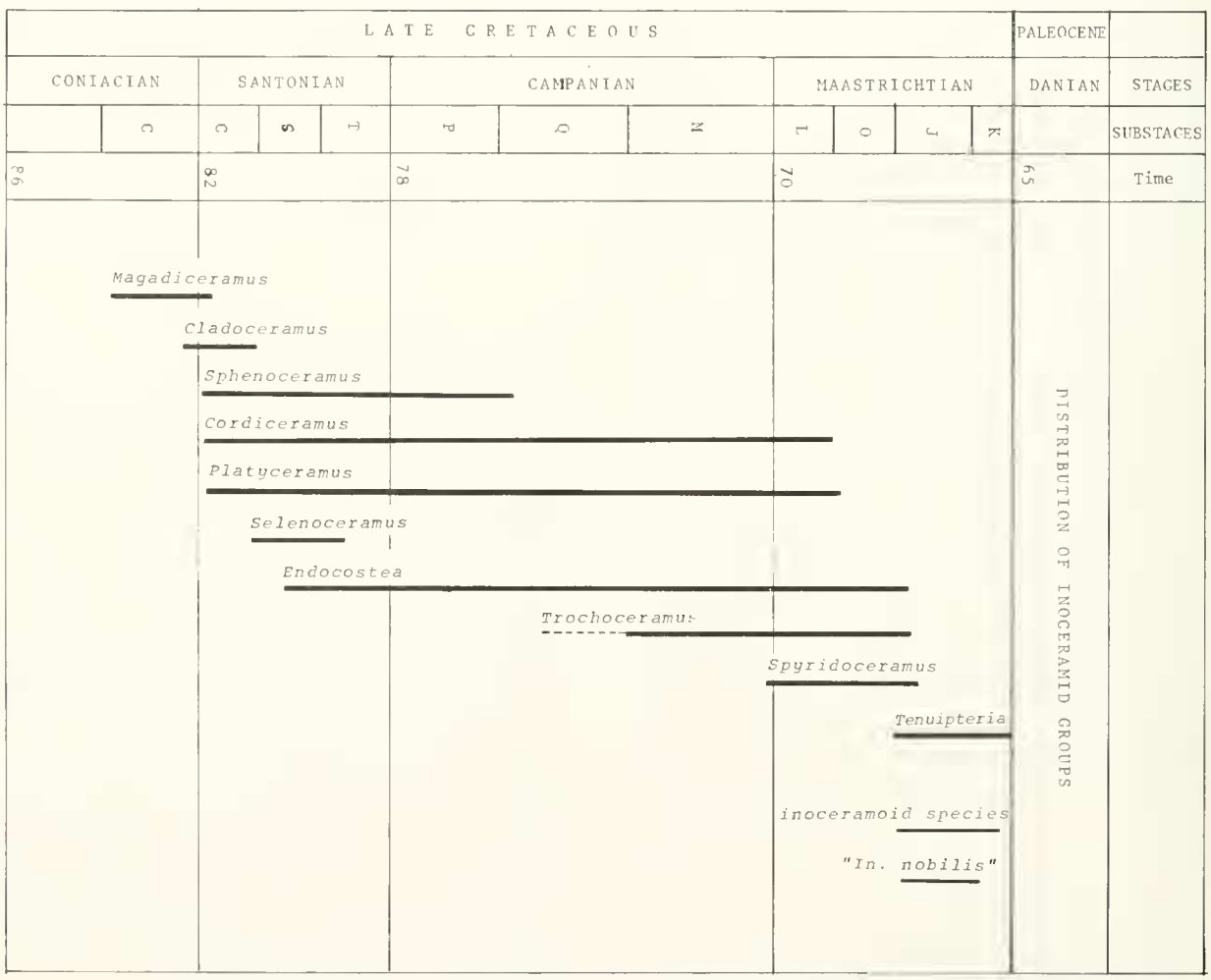

Fig. 1: Stratigraphic distribution of inoceramid "groups" between the Late Coniacian and Late Maastrichtian; symbols used: stratigraphical zones: Coniacian: C: *cortestudinarium;* Santonian: C: *coranguinum*, S: *socialis*, T: *testudinarium;* Campanian: P: *pilula*, Q: *quadrata*, M: *mucronata;* Maastrichtian: L: *lanceolata*, O: *occidentalis*, J: *junior*, K: *kazimirovensis*.

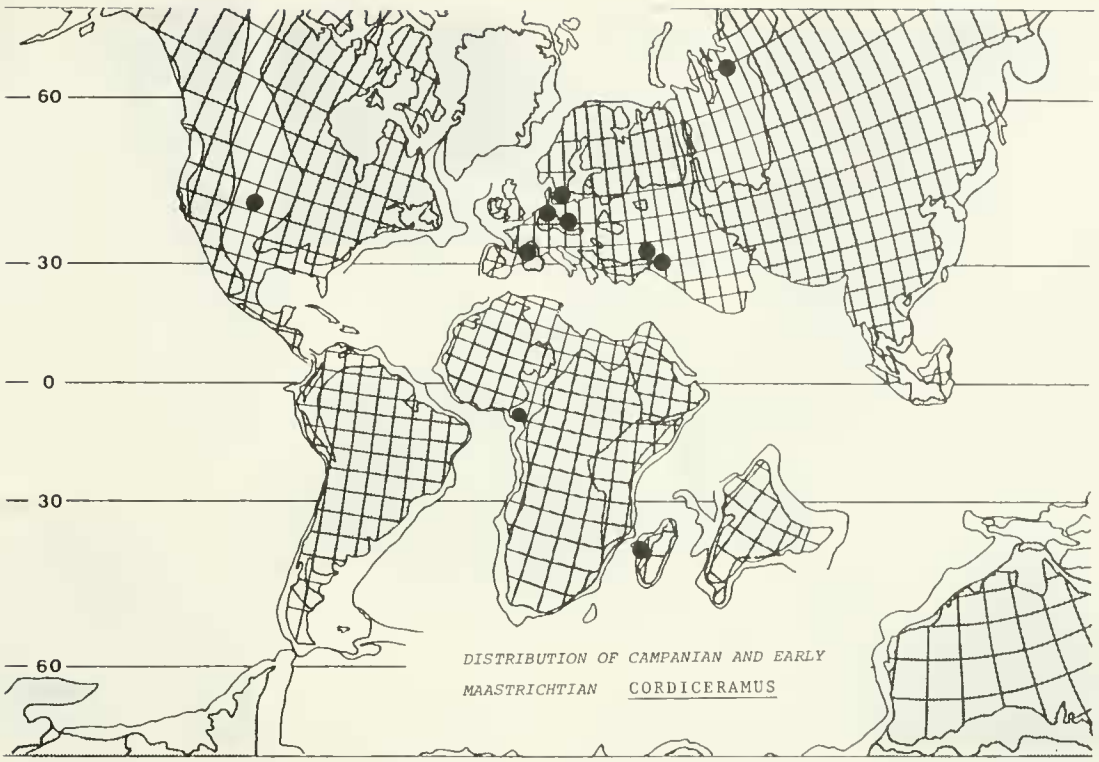

Fig. 2: Geographical distribution of Campanian and Early Maastrichtian *Cordiceramus* in the Euramerican Region, including the African and European Tethys; Map 80 mill. years out of BARRON et al., 1981.

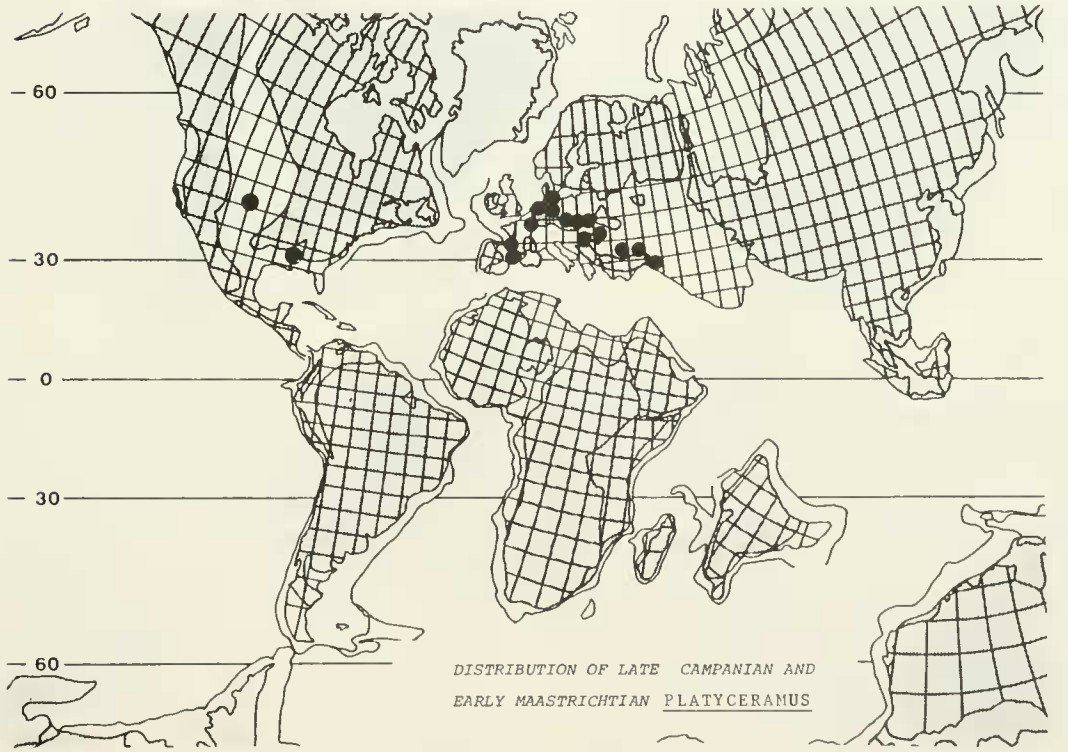

Fig. 3: Geographical distribution of Campanian and Early Maastrichtian *Platyceramus* in the Euramerican Region; map as on fig. 2.

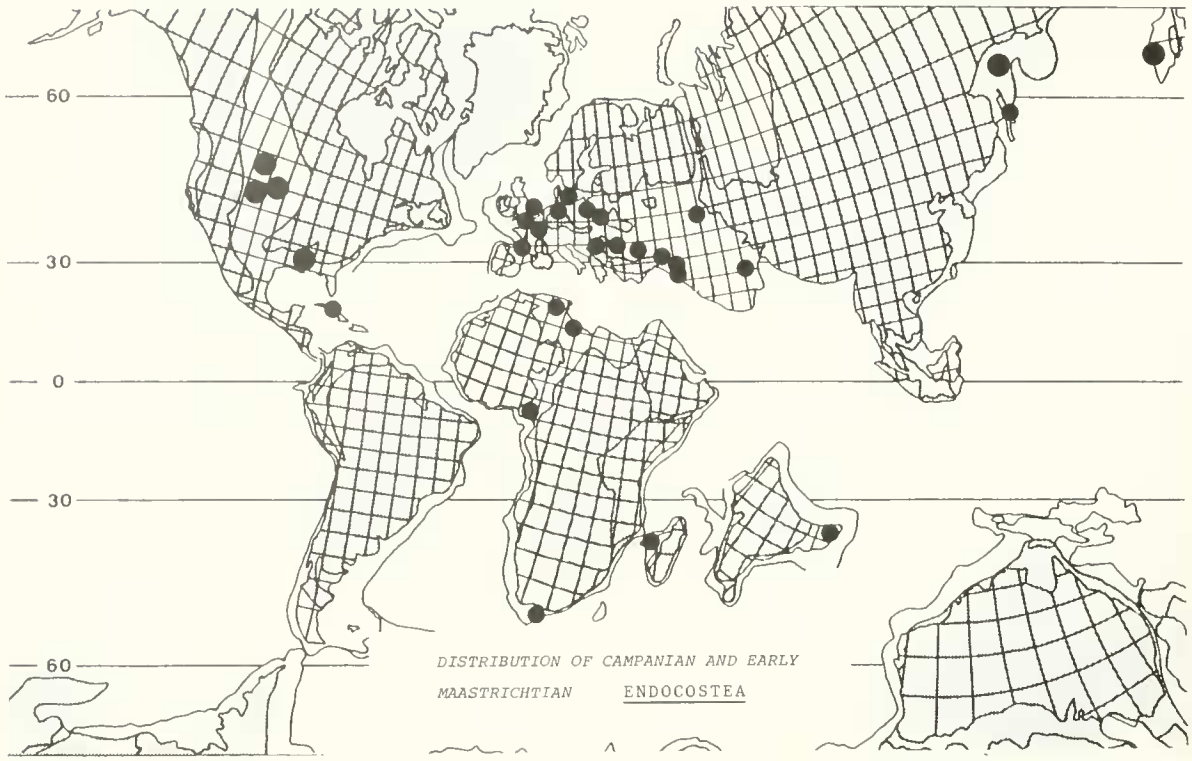

Fig. 4: Geographical distribution of Campanian and Early Maastrichtian *Endocostea;* map as on fig. 2.

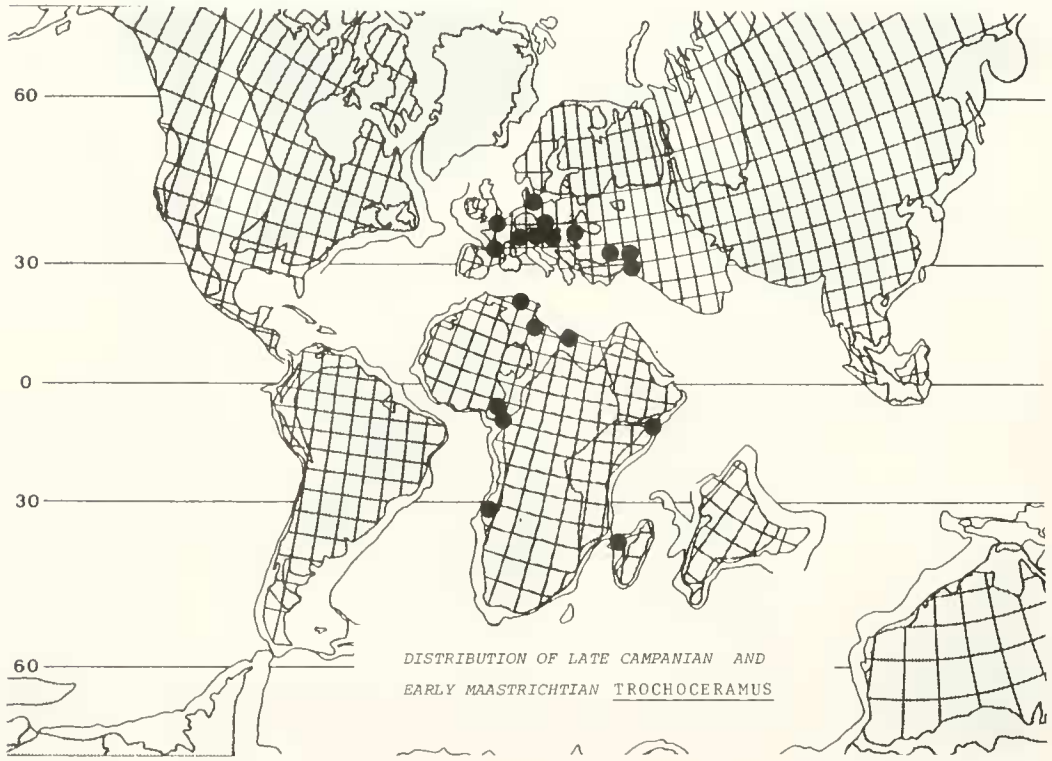

Fig. 5: Geographical distribution of Late Campanian and Early Maastrichtian *Trochoceramus;* map as on fig. 2.

Fig. 6: Geographical distribution of Maastrichtian *Spyridoceramus* and *Tenuipteria;* 1. *Spyridoceramus tegulatus,* 2. *Tenuipteria argentea,* 3. unidentified tegulated inoceramid; map as on fig. 2.

ted groups lived largely in temperate and cold temperate regions, as compared to the Tethyan occurrences of *Trochoceramus:* therefore it could be that this latters geographical limitation was more due to climatic grounds.

I have discussed elsewhere (DHONDT, 1983) why I consider *Spyridoceramus* and *Tenuipteria* as two different genera. Their distribution is more eastwest than in *Trochoceramus.* They seem to be largely and possible totally absent from the Tethys. The Upper Maastrichtian deposits of marine origin which we know in the area considered contain *Tenuipteria argentea* to the very youngest strata. Other definite Inoceramidae species are not known from Upper Maastrichtian strata.

IV. EXTINCTION OF INOCERAMIDS

In the Campanian-Maastrichtian we encounter the last representatives of the inoceramids. In traditional palaeontology we are taught that "at the end of the Maastrichtian inoceramids, along with the ammonites, rudists, dinosaurs, mosasaurs suddenly go extinct". As shown recently for many other groups this extinction was certainly not a "sudden" event, not even at the geologic scale (HANCOCK, 1967), ammonites (WIEDMANN, 1979), bivalves and other groups (KAUFFMAN, 1982), dinosaurs (SCHOPF, 1983), plants (CLEMENS, ARCHIBALD and HICKEY, 1981), general review (RAUP, 1982).

For the Inoceramidae the situation certainly follows the pattern of a gradual extinction as found in ammonites and dinosaurs. As shown on figure 1 no representative of the genus *Inoceramus* as traditionally understood has been found in Upper Maastrichtian strata. *Tenuipteria* is sufficiently different to have been considered separate by most inoceramid workers. Thus this youngest inoceramid genus is somewhat aberrant. The last *Tenuipteria* species, *Tenuipteria argentea* (CONRAD, 1858), is found until the youngest Maastrichtian strata at least in the Maastricht area and in Mangyschlack (USSR) (personal communication of Prof. D. P. NAIDIN, november 1981). One could argue that inoceramids of Late Maastrichtian age are rare because there are few deposits known of that age and hence there were fewer available niches for inoceramids. This explanation is at least partially unlikely because already in two instances inoceramid-like species have been found in Upper Maastrichtian deposits:

1. from the Koriak Mountainous region (Far Eastern USSR) *Korjakia kociubinskii* POCHIALAYNEN (1980) which has the general aspect of an inoceramid but has a different hinge and different shell structure,
2. from the Saint Pietersberg near Maastricht the species described by GOLDFUSS (1836) as *Inoceramus nobilis* MÜNSTER (p. 117, pl. 113, fig. 3, non *I. nobilis* MÜNSTER in GOLDFUSS, p. 109, pl. 109, fig. 4 from the Lias near Pyrmont). This species has the general aspect of a *Mytiloides.* Its hinge structure is unknown but the shell is definitely lacking a prismatic layer. The species is somewhat similar to

Neomoceramus IHERING, 1902 from the ?Oligocene of Patagonia (Argentina) as figured in the Treatise (COX in MOORE, 1969, p. N. 319, fig. C48,1).

Those species with an inoceramid-like appearance occurred in Upper Maastrichtian strata. They probably had the same mode of life as true Inoceramidae and simply took over the niches left empty by the disappearance of these. These replacing species do not seem to have been over-successful since they also are not definitely found in strata above the Upper Maastrichtian.

V. CONCLUSIONS

Inoceramids of Campanian-Maastrichtian age are not equally well studied in all regions of temperate and Tethys seas of the Northern Hemisphere. Stratigraphic correlation is not always as precise as could be desired and especially at the Campanian-Maastrichtian boundary the usage is not uniform – as a result it is often difficult to compare data.

At this point the following general conclusions can be drawn:

1. Biogeographically: in the Campanian-Maastrichtian interval two major regions have to be considered in the Northern Hemisphere:
   a) North Pacific Province as defined by JELETZKY, 1965,
   b) a region consisting of the Euramerican Region (as defined by KAUFFMAN, 1973) and of the Eurafrican Tethys (which included large parts of Africa not usually named "Tethys" such as the West and East African coasts). Faunistically the temperate seas and the Tethys seem to have many inoceramids in common.
2. Biostratigraphically: in the Campanian-Maastrichtian interval no inoceramid can be used on a wide scale for stratigraphic purposes. In the North Pacific Province endemic inoceramid species allow finer stratigraphic subdivision mainly in the Campanian. In the temperate seas of Maastrichtian age in the Euramerican region it is possible to differentiate by the presence of *Spyridoceramus* deposits of Early Maastrichtian age from those of Late Maastrichtian age which contain *Tenuipteria*. In the Tethys faunas from Europe and Africa no species has been encountered which allow to differentiate strata of Late Campanian age from those of Maastrichtian age.
3. Extinction: by Mid-Maastrichtian times all inoceramids except *Tenuipteria* had disappeared. At the beginning of the Maastrichtian several subgenera were still found but often the number of species belonging to them had strongly decreased since the Mid-Campanian. It was a gradual decline between the Mid-Campanian and the Mid-Maastrichtian. It seems likely that at the end of the Maastrichtian only one species of *Tenuipteria* was still extant. This species has not been found in the Danian strata which overlie the Maastrichtian strata in which it still occurred. In Late Maastrichtian times bivalves externally analogous to inoceramids are found. Possibly they took the niches left vacant by the disappearance of most inoceramids.

Abbreviations

B. M. (N. H.): collections of the Palaeontology Department, British Museum (Natural History), London, England.

I. R. Sc. N. B.: collections of the Palaeontology Department of the Institut royal des Sciences naturelles de Belgique- Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium.

ACKNOWLEDGMENTS

Part of the research for this paper was carried out in november 1981 – january 1982 during the tenure of an exchange fellowship of the Cultural Agreement USSR-Belgium (Internationale Culturele Betrekkingen, Ministerie van Nationale Opvoeding en Nederlandse Cultuur).

I would like to express my sincere gratitude to many colleagues who generously found time for helpful discussion, gave permission to study specimens in their care, provided information and/or gave guidance in the field: A. A. ATABEKIAN (Leningrad), Tove BIRKELUND (Copenhagen), W. A. COBBAN (Denver), R. A. GAMBASHIDZE (Tbilisi), J. M. HANCOCK (London), J. A. JELETZKY (Ottawa), E. G. KAUFFMAN (Boulder), W. J. KENNEDY (Oxford), N. J. MORRIS (London), D. P. NAIDIN (Moscow), J. M. PONS (Barcelona), F. SCHMID (Hannover), T. J. M. SCHOPF (Chicago), N. F. SOHL (Washington D. C.), J. SORNAY (Tain l'Hermitage), K. A. TROEGER (Freiberg), C. J. WOOD (London), T. D. ZONOVA (Leningrad).

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